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**Depth and vertical hydrodynamics constrain the size-
structure of a lowland streambed community**

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IPM, DP and ALR conceived the study. IPM, DP carried out the statistical analysis. Finally, IPM wrote the manuscript with a significant contribution from DP and ALR.

Title: Depth and vertical hydrodynamics constrain the size structure of a lowland streambed community

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Abstract: Abundance-body mass (N–M) relationships are prominent macroecological patterns and provide an integrated measurement of the structure and energy flow through natural communities. However, little is known about how N–M relationships are constrained by local environmental conditions. Here we quantify how sediment depth and direction of surface–groundwater exchange (vertical hydrodynamics), two major drivers of the streambed ecology, determine N–M scaling in a sandy lowland, European stream. Streambed assemblages included flagellates, ciliates, meiofauna and macroinvertebrates, and spanned five orders of magnitude in body mass. We detected a significant interaction of body mass with depth and vertical hydrodynamics with a sharp reduction in N–M slopes in the hyporheic zone and under upwelling conditions. These results revealed that streambed assemblages become more size–structured as environmental constraints increase with direct implications for the metabolic capacity and functioning of the system.

Keywords: Metabolic scaling theory, benthos, hyporheos, body size, freshwater communities

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1. Introduction

Abundance-body mass relationships are one of the most extensively studied patterns in ecological research [1,2,3] both in terrestrial and aquatic realms [4]. The distribution of the abundance (N) of organisms within body mass classes (M) on a logarithmic scale, known as the size spectrum (N–M relationship *henceforth*), provides an integrated measure of community size structure [5,6]. A gathering body of evidence demonstrates interactions between environmental stressors and N–M scaling coefficients [7], with N–M slopes typically becoming steeper following disturbances (e.g. [8,9]) – i.e. there is a relative increase in the number of small versus large organisms. This has led to the use of N–M scaling coefficients as a quantitative measure of deviation of a natural community from a reference status as a result of anthropic stressors [7]. However, little is known about how N–M scaling coefficients (intercept and slope) vary with persistent environmental gradients within natural systems, such as the availability of metabolic substrates and resources. These environmental factors are widely recognised as major selecting forces that determine which organisms survive and persist within a given habitat [9] and thus we might expect them to impact N–M scaling relationships.

In streams and rivers, empirical studies quantifying N–M relationships in the streambed have been limited to the upper sediment layer (benthic zone; e.g. [10, 11]). However, depth below the surface, and the direction of the surface–groundwater exchange (here as vertical hydrodynamics), have been widely recognised as primary ecological constraints shaping streambed communities and driving the ecological functioning of the streambed system at a micro–scale (see [12]). This is mainly because the reduction of oxygen and nutrient availability with increasing depth and under upwelling conditions limits the vertical colonization of organisms with larger body size and high metabolic requirements [13, 14, 15, 16]. Surprisingly little is known about how these environmental factors constrain N–M scaling in streambed systems but investigation into this question could provide important insights into the role of resource supply on community size structure [17].

Here we quantify for the first time how depth and surface–groundwater exchange (as vertical hydrodynamics) govern N–M scaling in streambed communities. We analysed data from a multi-disciplinary project in which community structure and magnitude of the surface–groundwater exchange were determined at a very fine spatial resolution (5 cm intervals) across a depth gradient in the streambed [12]. Streambed

assemblages included unicellular flagellates and ciliates, meiofauna (body length ranges between 0.45 and 500µm) and macroinvertebrates. We hypothesize that increasing streambed depth and upwelling groundwater exchange constrain the abundance of organisms, especially among large-size fractions as a result of reduced resource supply (i.e. oxygen) under these conditions. Thus we expect N–M intercepts (as a proxy of the carrying capacity of the community) to decrease, and N–M slopes (as a measure of energy flow and the trophic transfer efficiency) to become steeper, with depth and vertical hydrodynamics. Our findings shed light on how important environmental constraints may shape the structure, metabolic capacity and energy flow through streambed communities.

2. Methods

Data acquisition – Here we used open-access published data from Peralta–Maraver et al. [12], which included measurements of the vertical hydrodynamics quantified at the same spatial resolution as the community sampling. The assemblage of organisms and vertical hydrodynamic conditions in the streambed were sampled in six sites along a 3.5 km river stretch in the sandy river Erpe (northeast Germany). Even though the local scale of this study might limit the scope of our results, it allowed us to test the effects of depth and vertical hydrodynamics under natural conditions whilst controlling for other factors such as substrate type, community composition, stream temperature etc. Previous analyses using these data have focussed on the taxonomic composition, productivity and community delineation between benthic and hyporheic zones [12]; here we leverage these data, and a theoretical framework (abundance-body mass scaling), to assess, for the first time, the constraints of streambed depth and vertical hydrodynamics on community size structure and the transference of energy through the food web. A detailed description of the studied system and the sampling sites is available in the Supplementary methods.

Samples were collected weekly between 16th May and 16th June 2016. Using a modified Kajak corer, the assemblage of protists (flagellates and ciliates), meiofauna and macroinvertebrates inhabiting the sediments was sampled by slicing 5–cm layers down to 35 cm (7 depth-layers). Vertical hydrodynamics at each sampling site were characterised by coupling averaged measurements of the thermal extinction depth, vertical flux, and indirect analysis of redox conditions during the whole study period. Vertical flux was determined applying the Hatch amplitude method [18] and using

constant measures of streambed thermal depth profiles. These values ranged from negative values (upwelling conditions) to positive values (downwelling conditions), the value of 0 indicated no surface–groundwater interchange. In the laboratory, organisms were identified, counted and measured (length and width). Then, individual density (ind/L) was calculated and body dimensions of all counted organisms were converted to body mass ($\mu\text{g C}$). Additional details are provided in Supplementary methods and abundance and body mass values are available as Supplementary data.

Statistical analysis – We constructed N–M relationships for each sampling unit ($n = 168$: 6 sites \times 4 sampling occasions \times 7 depths). Size bins were created within the \log_{10} body mass range for each site and sampling occasion (variables fitted as random effects in the statistical models) and the abundance of organisms were summed within each size bin and regressed against the midpoint of each bin [19]. We used the logarithmic binning method for constructing size spectra [20], with equal bin widths on a log-scale. The number of bins ($n = 5$) was used as it maximized the number of size bins, while minimizing the number of empty size bins in the analysis [11,21]. The effects of streambed depth and hydrodynamics on N–M scaling was assessed by adding depth and vertical water flux as continuous covariates, as well as the interaction between them and with body mass, in the model equation. Detailed explanations of the binning method, model fitting and model validation is provided in the Supplementary methods.

3. Results and discussion

Over 5 orders of magnitude in body mass from flagellates to macroinvertebrates, abundance declined linearly (Fig 1a) with an average size spectra slope of -1.5 (Table 1). This slope [$N \sim M^{-1.5}$ (95% CI: -1.6, -1.4)] is much steeper than the generally assumed value of -0.75 or -1 within and across trophic levels, respectively [17]. Even when restricting our analysis to the top 5-cm depth and under downwelling conditions (the least constricting conditions), this observation was consistent (slope = -1.4, 95%CI: -1.5, -1.3). Therefore, our results support the notion that streambed and groundwater habitats are characterised by strongly size–structured communities [3,22].

As predicted, N–M intercept (carrying capacity) and slope (energy flow and the trophic transfer efficiency) were dependent upon depth and vertical hydrodynamics (Table 1). We found that the N–M intercepts were higher and slopes were indeed shallower under downwelling conditions (Fig 1a) and in the top sediment layers

(benthic zone; Fig 1b), while intercepts decreased and spectrum slopes exhibited a sharp decline under upwelling conditions and at deeper sediment layers (hyporheic zone). Moreover, both predictors showed a synergic interaction (i.e., the combined effect was more than the sum of its parts), on the N–M slope (Table 1). These results are consistent with the reduction in resource supply (e.g. oxygen) with depth and under upwelling conditions, which exert a greater selective constraint on large body–size classes [12,13]. We also verified whether our results were independent of the truncation of size spectra with depth – i.e. the largest body size organisms were not present at deeper sediment layers. For this purpose, we repeated the analysis including only communities from the upper 15 cm of the sediment – communities that spanned the full range of body size bins (Table S1) – obtaining similar results (Table S2). Given that metabolic rates scale with body size [25], and in the light of the decline in N–M intercepts with depth, the streambed assemblage also tends to be metabolically less active with increasing sediment depth. Crucially, our study shows that this is offset to some extent under down–welling conditions where the greater supply of resources allows larger organisms to persist [12,13,16,26].

Under equilibrium conditions, the slope of the size spectrum is expected to be described by the model: $N = M^\lambda \times M^{\log(\text{TE}) / \log(\text{PPMR})}$, where N is abundance of a given size class, M is body mass, λ is abundance–body mass scaling exponent within trophic levels, TE is transfer efficiency and PPMR is the predator–prey mass ratio [23]. Therefore an alternative explanation for the generally steep size spectra slopes observed in this study could be related to the trophic structure of the streambed community and changes in PPMR. Given the mean slope [$N \sim M^{-1.5}$ (95% CI: -1.6,-1.4)] we observed and a TE and λ value of 0.1 and -0.75, respectively [24], predator–prey mass ratios would be on average approximately 10:1 for this system. Such values are much lower than that observed for stream invertebrates [11] and lower than those expected from known predator–prey pairs in this study [e.g. Nematoda (mean = $3.5 \pm \times 10^{-1}$ mg/C) feeding on ciliates (mean = 2.3×10^{-5} mg/C)]. We propose therefore that differences in the trophic structure of streambed communities is unable to fully explain the steep N–M scaling in this study, but instead the reduction of resources with depth and upwelling conditions play a pivotal role in constraining the size structure of the streambed community.

The strong patterns reported here highlights that streambed communities become strongly size–structured as a consequence of the interplay between depth and negative vertical hydrodynamics, at least in lowland streams with sandy sediments. This

reduction in the number of large organisms also implies a concomitant reduction in the metabolic capacity of the system. These findings therefore highlight important constraints that govern the functioning of the sediments in streams and rivers that are key sites of intense biochemical turnover (including nutrients and pollutants) sustained and maintained by the metabolisms of the communities inhabiting them (see [16]). Our findings might therefore help explain why the biochemical turnover rates decrease markedly with depth [27], however, future research considering large-scale approaches is needed to extrapolate our findings to a more global context.

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Table 1. Summary table of the fitted abundance-body mass regression (fixed coefficients). Fixed coefficients (*Coef*), standard errors (*SE*), degrees of freedom (*DF*), *t*-values and P-values (*P*). Significance codes (*Sig*): 0 (***), 0.001 (**). A Satterthwaite approximation was used to calculate the effective degrees of freedom.

Fixed equation terms	Coef	SE	DF	t-value	P-value	Sig
Intercept	3.41	0.07	4.60	51.74	> 0.001	***
Log ₁₀ Body mass	-1.52	0.04	391.07	-37.74	> 0.001	***
Depth	-0.57	0.04	393.20	-13.78	> 0.001	***
Hydrodynamics (UW)	-0.33	0.09	3.89	-3.48	0.02	*
Log ₁₀ Body mass × Depth	-0.34	0.04	391.42	-10.06	> 0.001	***
Log ₁₀ Body mass × Hydrodynamics (UW)	-0.16	0.06	392.76	-2.51	> 0.02	*
Depth × Hydrodynamics (UW)	-0.16	0.07	394.10	-2.35	> 0.02	*

296 **Figure caption**

297 **Fig 1:** Multi-panel showing the results from the multiple linear regression of Log_{10} total
298 abundance on Log_{10} body mass bin, and the effects of vertical water flux (a) and depth
299 (b). In panels 'a' and 'b', each data point ($n = 457$) denotes the abundance of a given
300 size class for each sampling unit. The fitted lines in panel 'a' represent the average N-M
301 slope for upwelling (UW) and downwelling (DW) conditions, derived from the linear
302 mixed effect model. Note that the four obvious groups of data points in the panel
303 correspond to flagellates, ciliates and invertebrates meiofauna and macroinvertebrates.
304 The fitted lines in panel 'b' represent the average N-M slope in the upper sediment
305 layers (marked as BZ: benthic zone), and deeper sediment layers (marked as HZ:
306 hyporheic zone). The median value of depth (10 cm) was used as the midpoint between
307 BZ and HZ to simplify interpretation. Note that depth is a continuous covariate with a
308 three-dimensional relationship with the N-M intercept and slope (3d plot insert at the
309 top of panel b).

